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Superorganism resilience: eusociality and susceptibility of ecosystem service providing insects to stressors

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Insects provide crucial ecosystem services for human food security and maintenance of biodiversity. It is therefore not surprising that major declines in wild insects, combined with losses of managed bees, have raised great concern. Recent data suggest that honey bees appear to be less susceptible to stressors compared to other species. Here we argue that eusociality plays a key role for the susceptibility of insects to environmental stressors due to what we call superorganism resilience, which can be defined as the ability to tolerate the loss of somatic cells (=workers) as long as the germ line (=reproduction) is maintained. Life history and colony size appear critical for such resilience. Future conservation efforts should take superorganism resilience into account to safeguard ecosystem services by insects.

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Introduction

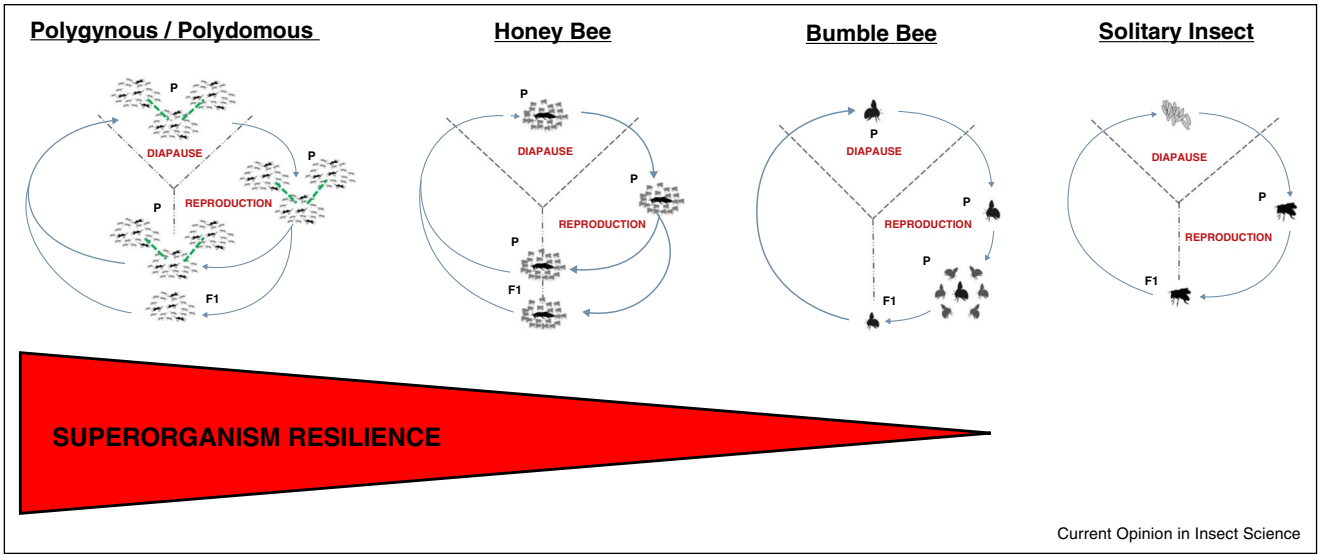
In terrestrial ecosystems, insects are a dominant and diverse group that displays a diverse array life history strategies, ranging from solitariness, through gregariousness to eusociality [1]. Several different insect genera contribute to essential ecosystem services, including pollination and natural pest control, which are vital to supporting global biodiversity and human food security [2–4]. Consequently, major declines of wild insects providing such ecosystem services, in combination with elevated losses of managed honey bees, throughout the northern hemisphere are of widespread concern [3,5]. Habitat destruction [6], invasive species [7,8], and climate change [9] seem to play key roles, but susceptibility to other stressors (e.g. pathogens and pesticides) may equally contribute [10,11]. Hence, there is a need for appropriate insect conservation strategies [12,13]. Recent data [14••,15••] suggest that eusocial honey bees appear to be less susceptible to stressors compared to bumblebees and solitary bee species; this might be due to different abilities to detoxify and thus withstand pesticide stress [15••,16]. However, regardless of potential differences in the ability of individuals to tolerate environmental stressors, we here address the roles of eusociality and life history as fundamental biological factors that govern the buffering capacity of insect species (Figure 1).

Superorganism resilience and colony size: bigger is better

Eusocial insects live in colonies that are characterized by reproductive division of labour among females (and males in termites), overlapping generations and cooperative brood care [17]. With some exceptions (e.g. ponerine ants [18]), queens usually monopolize reproduction (=primary reproductive females that can produce diploid offspring) whilst workers carry out all other tasks required to maintain the colony. Worker duties include more risky tasks such as foraging, which exposes them to stressors outside of the nest (e.g. pesticides [19]). Solitary species lack these characteristics, with each individual directly contributing to reproduction. Since workers usually do not reproduce, the death of such a single individual does not necessarily compromise colony reproduction, and hence fitness. Nevertheless, depending on the species, a minimum number of workers are required to ensure and maintain colony functionality and reproduction [20]. For example, in honey bees, *Apis mellifera*, a minimum of 100 workers is required for efficient brood rearing [20].

Since eusocial insect colonies are considered to be superorganisms [21], workers can be viewed as analogous to somatic cells in a metazoan organism. Like metazoans, superorganisms can tolerate and buffer against losses of somatic cells as long as colony functionality and the germ line are maintained [22••]. This is the fundamental factor constituting superorganismic resilience. However, this buffering capacity relies on a range of factors and may vary (e.g. according to season). In temperate regions, honey bees overwinter as colonies, which makes thermoregulation essential [21]. To ensure efficient thermoregulation and survival, a certain colony size is required [23] which exceeds the bare minimum colony functionality in

Figure 1



Eusociality, life history and relative superorganism resilience in insects. The four major groups, their life history and relative superorganism resilience are shown. Polygynous and polydomous species with large perennial nests and dependent nest founding possess the largest superorganism resilience (some ants). Monogynous, monodomous species with large nests and dependent nest founding are less resilient (e.g. honey bees). Species with a solitary phase (e.g. during diapause) and independent nest founding as well as small colonies are even more vulnerable (e.g. bumblebees). Lastly, solitary insects have no superorganism resilience, because each female is reproductive. Black irregulars, sexual reproductive; grey irregulars, workers; blue lines indicate life history development, green lines indicate connection between nests, P, parental; F1, first filial).

spring and summer. Colony size varies considerably in eusocial insects, ranging from less than a dozen workers in ponerine ants [24] to millions of workers in leaf-cutting ants [25]. Colonies of *A. mellifera* honey bees are typically two orders of magnitude larger than *Bombus terrestris* bumblebees during the foraging season [26]. Such variability in colony size appears to play an important role for resilience of superorganisms because demographic and environmental stochasticity has in general a much larger effect on smaller populations [27,28]. By chance alone, a few workers might be affected by a stressor and thereby endanger a small colony. Indeed, larger size can increase colony survival in honey bees as well as ants when confronted by stressors [22••,23]. Furthermore, the ability of eusocial colonies to store food reserves over longer periods of time (e.g. diapause) or in arid seasonal phases is a crucial factor for colony survival. It appears apparent that solitary living species have an obvious disadvantage, such as when weather conditions do not afford foraging. However, not all social living insects have equal capacity to buffer against stressors; individual life histories of each species appear to also play a decisive role.

Life history

With the exception of mating flights, queens of some species (e.g. genus *Apis*) reside among nestmates for their entire life, wherein a court of worker attendants tends to their nutritional and hygienic demands [21,26]. Therefore, queens appear to be sheltered and not confronted with stressors to the same degree as other nestmates. Conversely, *Bombus* bumblebee queens usually live only part time in such a protected colony environment [21]. Mated bumblebee gynes (=future potential queens) overwinter as individuals prior to solitary colony initiation in the following spring. This solitary phase constitutes a significant bottleneck as it exposes females to numerous stressors throughout the diapause period. Moreover, in several species of the social insects like ants (e.g. *Lasius* spp.), bees (*Bombus* spp.) and wasps (e.g. *Vespa* spp.), queens start new nests independently [26], which constitutes another solitary phase. Queens searching for a suitable nest site or forage results in higher exposure of the female sexuals to stressors compared to dependent nest foundation in swarming bees (*Apis* spp. and stingless bees) and ants (e.g. in some *Formica* species; [26]). Therefore, it appears as if eusocial insect species which have perennial colonies over many years (e.g. *Apis*) possess a higher superorganism resilience compared to those which have annual nests (*Bombus* spp.). However, despite being sheltered by workers, queens may nevertheless be affected by stressors, which is crucial because the role of queens in social insect colony survival is indispensable. Indeed, the usually long lived queens can be exposed to stressors over long time periods (e.g. pesticides) and may succumb to them throughout the year (e.g. queens in *A. mellifera* [29,30••]). The successful development as well as successful mating flights for queens trigger molecular, physiological and behavioural changes which enhance their survival [21,31]. Previous investigations have observed that

bumble bee colonies exposed to neonicotinoids produced fewer gynes (future queens) [32,33] and that honey bee colonies replaced queens more frequently [29]; however, mechanisms responsible for these observations have not yet been identified. In any case, the loss of queens seems to be weak point of superorganism resilience; therefore, eusocial insect species that are capable of replacing dead or diseased queens (e.g. from young female larvae in *Apis* spp. [21]) are substantially more advantaged compared to others that cannot (e.g. leaf-cutting ants *Atta* [34]). In addition, the sheer number of queens present within a colony may also have a significant effect on the improved susceptibility towards stressors. Monogynous species with a single queen (e.g. *Apis*) may be more at risk compared to polygynous ones (e.g. *Formica*), especially when there are no options for the colony to replace the queen (e.g. during the winter broodless period in honey bees). Therefore, polygynous species may have an even more adaptive system to buffer stressors because the loss of a single or even multiple queens can be tolerated by the colony. Finally, social insect species with both multiple queens and multiple nesting sites (=polydomous [26]) would be expected to have the best opportunities to buffer against various stressors. Hence, even if an entire individual nest succumbs to any given stressor, the overall colony will survive.

In sharp contrast to social species, solitary insects are exposed to all of the above addressed issues, and thus probably follow a more risk-sensitive strategy such as adjusting the sex ratio of their offspring in response to stressors [29]. Even if a species may show gregariousness, with hundreds of individual nests in close spatial prxiomity (e.g. due to nest site limitations [1]), the individual females are nevertheless responsible for their own offspring. It appears as if a more diverse immune repertoire may be required in solitary species. Indeed, the similarity in immune complement across a gradient of sociality suggests that a reduced immune repertoire predates the evolution of sociality in bees [35••]. Therefore, the ability to tolerate stressors has to be regarded across social contexts. Social insect superorganisms have uniquely evolved both individual and social disease resistance strategies that are not observed in solitary species. Examples include allogrooming (i.e. intraspecific cleaning of nest mates) [36] and social analogues to the immune system of vertebrates, such as behavioural fever (i.e. changing nest temperature to defend against microorganisms) [37] and social encapsulation [38].

Conclusion

Here we provide a framework for the apparent buffering capacity of eusocial insect species towards various different stressors. In contrast to social immunity, there are no interactions required among nest mates for superorganismic resilience. This buffering capacity can occur intentionally or non-intentionally. In the case of altruistic suicide behaviour, health compromised honey bee workers leave the nest to prevent the spread of illness or ant workers scarify themselves to defend the nest [39,40]. Non-intentional superorganismic resilience is demonstrated when, for instance, a colony is exposed to pesticides and the affected individuals simply die. In brief, a strong colony will be able to buffer these losses and survive.

This superorganism resilience contributes to our understanding of the global success of social insects, thereby reinforcing that the benefits of social living clearly outweigh its costs [19]. Considering the vast biological differences among insects, we argue that an emphasis on establishing additional indicator and model species for the study of environmental health is warranted and urgently required. Superorganism resilience constitutes a significant buffering capacity, especially for larger colonies, and may not mirror strong effects of stressors on other ecosystem service providing species (e.g. in the case of pesticides [15••]). We therefore stress the need to include non-*Apis* species in future risk assessment and for further studies on the effects of environmental stressors (e.g. parasites) acting alone and in combination [41] at the individual and colony levels. Protecting honey bees alone, or even other charismatic eusocial species, will not be sufficient to protect ecosystem services provided by insects. Adequate insect conservation should take into account superorganism resilience.

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This report by the European Academies Science Advisory Council overviews the state of modern agriculture and its reliance on ecosystem services. The authors pay particular attention to the use of neonicotinoids for managing insect pests. They conclude that these insecticides have wide-ranging effects on beneficial organisms and that their prophylactic use contradicts the basic principles of the EU's Sustainable Pesticides Directive that promote integrated pest management in agriculture.

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